

2.—Studies in the Water Relations of Plants

1.—Transpiration of Western Australian (Swan Plain) Sclerophylls

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The water economy of character plants of the hard-leaved evergreen vegetation on the Perth coastal plain has been studied to obtain information on their behaviour both before and during the long dry summer. With the exception of *Eucalyptus marginata*, all the sclerophylls so far tested (e.g., *Banksia menziesii* and *B. attenuata*, *Stirlingia latifolia*, *Hibbertia hypericoides*, *Bossiaea eriocarpa*, *Hardenbergia comptoniana*, *Kennedya prostrata*, *Eucalyptus calophylla*, *Xanthorrhoea preissii*, *Petrophila linearis*) showed in greater or less degree decreasing rates of transpiration with increasing dry conditions. In the spring, transpiration was high, curves being of the one-peak type in *Bossiaea*, *Kennedya*, *Banksia attenuata*, *Hardenbergia* and *Stirlingia*. In summer, curves were commonly of the two-peak type, while in late summer values for some plants remained very low throughout the day after an early morning peak. Average rates of water loss seldom exceeded 5-6 mg./g./min. during the summer. The relatively shallow rooting *Hibbertia* and *Bossiaea* in particular showed very low values and passed into a state of near dormancy in late summer. The moisture content of soil at this time is low, while the soil suction force rises above the osmotic values of the leaves. The plants remain in a condition of severe water stress until the break of season rains. The tree sclerophylls, *Banksia* spp. and *Eucalyptus calophylla*, and the shrubs, *Stirlingia*, *Hardenbergia* and *Kennedya*, with both a shallow and a deep root system, reduced their transpiration rate in summer but were not under conditions of marked water stress. Stomatal movements in some plants (e.g. *Hibbertia*, *Bossiaea*) showed reasonable correlation with rate of water loss; in others (e.g. *Stirlingia*) stomata remained open at the University station while transpiration rate was falling. Under the more desiccating conditions at the Cannington station they remained closed during the day. A higher rate of transpiration was found in older leaves (as against those of the current season flush of growth) in such plants as *Banksia* and *Stirlingia*. Slower photo and hydro-reactions were observed in stomata of such older leaves. Cuticular transpiration was found to proceed at a low level in the more highly cutinized sclerophylls. The osmotic values of leaves rose with advancing summer, while a rapid return to lower values occurred with break of season rains. Experiments to determine relative xerophytism have so far yielded inconclusive results owing to difficulties with water uptake by the cut-off leaves. Colateral studies on non-sclerophyllous shrubs which grow on the Perth coastal plain, indicate that a considerable degree of physiological diversity exists. *Phyllanthus*, for example, with its soft thin leaves shows a high rate of water loss in spring and early summer. With increasing dryness it maintains its water balance by shedding its leaves. A mesomorph, *Erechthites hispidula* maintained a high rate of transpiration in spring and in summer up to the time it died off.

Introduction

Relatively little information is available on the water economy of Australian sclerophylls under field conditions, the work of Wood (1923, 1924, 1934) in South Australia, standing alone in this regard.

In an effort to extend our knowledge of this aspect of the physiology of the sclerophyll plants of Western Australia, transpiration and associated studies were planned for stations passing progressively inland from Perth on the western coast towards the Eremaea. From these experiments it is hoped to determine the degree of physiological diversity existing among the sclerophylls and to ascertain the nature of possible ecological adaptations. In the present paper the results obtained for the first stations on the Swan Coastal Plain are presented.

The Research Area—Its Vegetation and Soils

The affinities of the sclerophyllous trees and shrubs of the Swan Coastal Plain were indicated by Diels (1906) who referred to them as "thick shrub growths which can be compared with the maquis of the Mediterranean or better still with the stiff-leaved scrub of the Cape." The plants are predominantly hard-leaved and evergreen, herbaceous plants being poorly represented. Two stations were selected for the study of character plants—one in the vicinity of the University, and the other at Cannington a few miles south-east of Perth—so that these observations are representative of the vegetation of the metropolitan sector of the Swan Plain.

The tree community near the University is of mixed Jarrah (*Eucalyptus marginata*), Marri (*Eucalyptus calophylla*), *Banksia* and *Casuarina*. The associated shrub layer consists mainly of sclerophyllous plants varying from tall shrubs (± 10 feet in height) down to shrubs ($\pm 2-3$ feet in height). Herbs, varying in height from two to three feet down to a few inches, occur in the shrub layer.

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The soil at the University station may be described as greyish-yellow to yellow sand (Karrakatta Sand). It is neutral or very slightly acid in reaction and the surface soil is darkened with organic matter. The soil profile in the main area of study is as follows:—

Sparse litter

Greyish black—0in.-8in. Coarse sand containing organic matter

Greyish yellow—8in.-18in. Coarse sand

Light brownish-yellow to yellowish-white, changing to yellow with depth—18in.-84in. Coarse sand containing a moderate amount of ferric oxide.

The climax community on the sandy ridges at Cannington is *Banksia* low scrub forest with associated shrub and herb layers. A typical soil profile (Speck, 1952) in the Muchea sands of the area is as follows:—

A₀ Sparse litter

A₁ 0in.- 3in.—Grey sand with little organic matter

A₂ 3in.- 8in.—Light grey sand—becoming leached

8in.-60in.—Highly leached white sand

B₁ 60in.-70in.—Definitely darkened layer of brown sand suggesting a slight tendency towards formation of Coffee rock

70in.-80in.—Yellow brown clay streaked with blue at depth

Several of the species selected for study were common to each station. Those at Cannington showed in general a higher degree of xeromorphy.

Climate

The Perth area possesses a typical Mediterranean climate, the summers being long and dry, while the rain falls during the mild winter period. The rains commence in May and increase in intensity during June and July. In August there is a slight falling off and during September and October the rainfall decreases still further. This winter rainfall accounts for just over 30in. of the annual average of 34.7 in. Scanty rain (mean value rather less than 1in.) occurs during November, while December, January, February, March and most of April are dry months with rainfall average usually well under 1in. Evaporation figures during this

period are high. Gentilli (1948, 1950) from a study of climatic data considered that under the conditions of high evapo-transpiration and little rainfall of the five summer months, the native vegetation in the Perth area would be under stress. Speck (1952) from observations on soil moisture content in the Cannington area in early summer also suggested that plants there would be subject to conditions of water stress for several months.

Methods

Measurement of Transpiration

Transpiration measurements were made using Huber's (1927) "quick weighing" method in which the loss of weight in the first 2-3 minutes after the leaf has been severed from the plant is considered to represent the natural transpiration. This method has been widely used in ecological and physiological work but has been the subject of much discussion and criticism. The main criticism has been that with the rupture of the water columns, on cutting, the release of stress would cause the water to rush upwards so that the leaf would temporarily be supplied with more water, leading to heightened transpiration. Ivanoff (1928) found such an increase in transpiration and various other workers including Kamp (1930) Weinmann and Le Roux (1946) and Anderson, Hertz and Rufelt (1954), have also recorded such an effect. Rouschal (1938) working with northern Mediterranean sclerophylls reported that with one exception there was a regular fall on weighing after abscission, while Oppenheimer (1953) working with similar plants in Palestine reported a regular decrease with time in some species tested and considerable irregularity in others. Our experience here has been that some species tested in summer showed a slow consistent decline in weight over successive two-minute periods, e.g., *Hardenbergia*, *Bossiaea*, *Phyllanthus*; while others sometimes showed a suggestion of the Ivanoff type of increase followed by a consistent fall, e.g., *Hibbertia*. In others again (and this applied more particularly when older leaves were under test) the rate of water loss was somewhat irregular, but remained fairly high over a period of several minutes, e.g. *Stirlingia*, *Banksia*... Typical results for water loss over the first few minutes are given in Table I.

TABLE I
Water Loss from Freshly Cut Leaves

<i>Hardenbergia comptoniana</i>		<i>Bossiaea eriocarpa</i>		<i>Hibbertia hypericoides</i>		<i>Stirlingia latifolia</i>		<i>Banksia attenuata</i>	
Time	Loss (mg.)	Time	Loss (mg.)	Time	Loss (mg.)	Time	Loss (mg.)	Time	Loss (mg.)
12.10	15.5	14.50	12.10	12.40
12.12	2.1	15.7	1.8	14.52	2.0	12.12	1.5	16.12	3.0
12.14	1.8	15.9	1.2	14.54	1.7	12.14	1.2	16.14	2.8
12.16	1.7	15.11	0.4	14.56	2.3	12.16	1.1	16.16	3.1
12.18	1.3	15.13	0.2	14.58	1.2	12.18	1.0	16.18	2.6
12.20	1.3	15.00	1.0	12.20	1.0	16.20	2.7
12.22	0.9	12.22	0.7	16.22	2.4
....	12.24	0.6	16.24	2.1
....	16.26	2.4

From these and other results it was considered that the most reasonable measure of the rate of transpiration for the purposes of this ecological study would be during the first two minutes. The downward trend was fairly general after this time, while the Ivanoff type of increase, when it occurred, was seldom apparent before the first two minute reading. It is held that the method is basically sound as well as being at present the most appropriate for field studies on transpiration.

The torsion balance used by the author was an Oertling P type (100 mg.) with a milligram scale and mirror so that readings could be made to an accuracy of 0.2 mg. Leaves were cut from the plant with a vaseline smeared razor blade and suspended from the balance hook by means of standard weight cotton threads. Hinged compartments on the balance eliminated wind effects on leaves and counterpoises at the moments of original and final weighing, the leaves being fully exposed for the 2 (or in some experiments, 3) minutes specified. A stop watch was used for timing. Parallel measurements, with as short a time as possible between them, were made with at least two leaves (opposite leaflets in the case of *Hardenbergia* and *Kennerdya*) which were similar in age, and position on the test plant.

Transpiration rate is expressed in terms of fresh weight as mg./g./min., and in terms of surface area [total area of leaf (cf. Rouschal, 1938)] as mg./sq. dm./min. where the leaf outline could conveniently be drawn and its area obtained with a planimeter. Transpiration records were obtained on selected days during most months of the year. More numerous experiments were done during the period of change from the wet to the dry season.

Evaporation

Evaporation was measured using Stocker's method (1929) as revised by Stahlfelt (1932). The evaporation from a filter paper disk (area 27.7 sq. cm.) during a period of 1-2 minutes was obtained, readings being made at hourly or other intervals as required. These served to give values which were more readily comparable with transpiration from test plants. Piché atmometers as described by Walter (1929) were used to obtain a continuous record of evaporation.

Water Saturation Deficit

Stocker's method (1929) was followed for the determination of the water saturation deficit with the modification that the petioles were cut once only. After a saturation period of 24 hours the leaves were re-weighed and then dried to constant weight at 100°C. The initial and maximum water contents were obtained by subtracting the dry weight from the initial and maximum fresh weights and the water saturation deficit calculated as follows:—

$$\text{W.S.D.} = \frac{\text{Maximum water content} - \text{Initial or field water content}}{\text{Maximum water content}} \times 100$$

Sub-Lethal Water Deficit

As well as determining the Water Saturation Deficit of the leaves in the course of a day during summer, it is necessary to know how much

water the leaf is able to give off without undergoing severe injury. This necessitates the continuation of a drying out process sufficiently long for the first signs of death of cells to be recognized. Oppenheimer (1932) coined the expression Sub-lethal Deficit for this and Rouschal (1938) applied the method in detail to the sclerophyll vegetation near Rovigno on the north-eastern Adriatic coast. The Sub-lethal Deficit may be defined as the maximum water deficit which the leaf will stand without death of more than $\pm 5\%$ of leaf tissue. The concept is useful in that it allows us to determine how close to the actual danger point natural water loss from the leaf may go and thus gives more precise meaning to the leaf Water Saturation Deficit.

Following Rouschal (1938), the procedure was adopted of rapid torsion balance weighing of 8-10 separate leaves of a selected plant, then allowing them to dry gradually in air. Periodically (intervals of 30 minutes were in general found to be suitable) a leaf was taken and re-weighed, notes being made on changes in colour or appearance. The petiole was then slit longitudinally and the leaf placed in water. After 2-3 hours under humid conditions it was re-weighed to determine whether water uptake was occurring and finally it was dried to constant weight. This procedure was continued for successive leaves until the point was found where even while some water was still being taken up, death of $\pm 5\%$ of cells was occurring. Determination of this sub-lethal point presented some difficulty as Rouschal's criteria for estimating death of cells namely healthy tissue appearing clear, and moribund tissue cloudy when viewed in transmitted light, proved unsuitable for most of the sclerophylls examined. Parker's tetrazolium chloride test (1951, 1952) while offering advantages for precise measurement of the lethal level was unsuitable for the determination of the sub-lethal level required. Reliance was finally placed upon changes in shape and colour in the leaves and on marked diminution of their ability to take up water after a certain period of drying out.

$$\text{Sub-lethal Deficit} = \frac{\text{Saturation water content (Max. water content)} - \text{Dried out water content } (\pm 5\% \text{ cells dead})}{\text{Maximum water content}} \times 100$$

The natural Water Saturation Deficit, which is obtained from additional leaves at the same time as the above, may then be compared with the Sub-lethal Deficit and expressed in per cent of this, i.e.

$$\frac{\text{Natural Water Saturation Deficit}}{\text{Sub-lethal Deficit}} \times 100$$

Stomatal Aperture

Schorn's (1929) series of infiltration liquids (isobutyl alcohol and ethylene glycol in 11 mixtures varying from pure isobutyl alcohol, through isobutyl alcohol 9: ethylene glycol 1, isobutyl alcohol 8: ethylene glycol 2, etc. to pure ethylene glycol) was found to be reasonably successful for a number of sclerophylls.

Alvim and Havis's (1954) method of using *n*-dodecane-nujol in a series of ten concentrations in steps of 10% by volume from pure *n*-

dodecane to pure nujol was also used in later experiments and proved valuable in demonstrating smaller stomatal apertures than the Schorn series could record. It also gave more detailed information on slight changes in stomatal aperture. With some plants, however, difficulty was experienced in obtaining as clear a reading as with the Schorn series because of the lack of contrast between the infiltrated and non-infiltrated areas.

Light Intensity

Light intensity was measured in foot candles by means of an EEL photoelectric meter fitted with suitable filters.

Temperature and Relative Humidity

Temperature and relative humidity of the air were measured using a Sling Psychrometer. Instead of Relative Humidity, results are expressed in percentage Saturation Deficit (100-RH) as this latter, as Oppenheimer and Mendel (1939) point out, is in direct relationship to the intensity of transpiration and evaporation.

Soil Suction Force

The suction force of the soil was determined using the method of Gradmann as modified by Heilig (1931). The method proved suitable when the moisture content of soils was reasonably low, but in the absence of a suitable constant temperature room difficulty was experienced in making measurements of low suction tensions because of the condensation of moisture on the walls of the vessels and on the strips of filter paper when the vessels were taken out of the incubator to carry out weighings. It is believed that moisture in soils at this stage is readily available to the plant, forces of not more than 2 atmospheres being involved in binding the moisture to the soil.

Soil Moisture Content

Samples were taken at 1 foot and 2 feet depth in the vicinity of test plants. 10 g. of soil were weighed, then dried to constant weight. The difference between the fresh weight and the dry weight multiplied by 10 gave the percentage of moisture in the soil (Piper, 1944).

Periodicity, Leaf Anatomy and Root Systems

The following sclerophylls were used in this study of water economy:— *Banksia menziesii*, *B. attenuata*, *Stirlingia latifolia*, *Bossiaea eriocarpa*, *Hibbertia hypericoides*, *Eucalyptus calophylla*, (these species were common to both the University and Cannington stations), *Eucalyptus marginata*, *Hardenbergia comptoniana*, *Kennedya prostrata*. In addition periodic observations were made on sclerophylls such as *Daviesia nudiflora*, *Xanthorrhoea preissii*, *Acacia cyanophylla* and *Conostephium pendulum* and on the tomentose succulent *Scaevola canescens*, together with the glabrous, semi-succulent *Scaevola paludosa*, *Phyllanthus calycinus* (a soft-leaved but xerophytic plant), and the mesophyte *Erechthites hispidula* completed the types of plant studied.

Periodicity

A feature of the growth of sclerophylls such as *Banksia* spp. is the spring flush of growth which continues into early summer by which time the leaves are reaching maturity and have become thick and hard. *Hibbertia*, *Bossiaea* and *Phyllanthus* commence their new growth early in winter and continue through to early summer, while in *Stirlingia* the growth flush begins in late spring or early summer and leaf development continues well into the dry season. *Hardenbergia* shows no marked periodicity of growth, new leaves continuing to appear throughout the summer.

Ecological Anatomy—Structure

The mature leaves of *Banksia* species show a thick cuticle on the upper surface and densely matted hairs covering stomata on the lower surface; *Hibbertia*, *Bossiaea*, *Hardenbergia* and both species of *Eucalyptus* studied show a strong development of cuticle with stomata restricted to the lower surface; *Stirlingia* with vertically growing leaves and overall cutinization has stomata present on both surfaces; older *Kennedya* leaves are strongly thickened with stomata present on both surfaces but more numerous per unit area on the lower surface, while in *Phyllanthus* the leaves are thin and soft, the relatively few stomata per unit area being restricted to the under surface. In Table II the structural characteristics of the sclerophylls tested are given according to the scheme of Evenari (1938).

TABLE II
Anatomical Features of Sclerophylls

	<i>Banksia menziesii</i>	<i>Banksia attenuata</i>	<i>Stirlingia latifolia</i>	<i>Hibbertia hypericoides</i>	<i>Bossiaea eriocarpa</i>	<i>Eucalyptus calophylla</i>	<i>Eucalyptus marginata</i>	<i>Hardenbergia comptoniana</i>	<i>Kennedya prostrata</i>
Thick and entinized epidermis	+	+	+	+	+	+	+	+	+
Cover of thick hairs on lower surface of leaf	+	+	—	Dense stellate hairs	—	—	—	—	—
Depression of stomata	±	±	—	—	—	—	—	—	—
Small inter-cellular spaces	+	+	+	+	+	+	+	+	+
Well developed mechanical tissues	+	+	+	+	+	+	+	+	+
Isobilateral structure of leaves	—	—	+	—	—	—	±	—	—
Reduction in size of leaves	—	—	—	+	+	—	—	—	—
High number of stomates per unit area (sq. mm.)	+	+	—	—	+	+	Medium	Medium	Medium

Root System

In *Hibbertia* the root system is relatively shallow, being contained in the first two feet of sandy soil. In *Bossiaea* and *Kennedya* the roots are somewhat deeper penetrating, while in *Stirlingia* in addition to a well branched shallow rooting system a main root goes down to considerable depth. In one instance such a root was traced to over 8 feet without appreciable diminution in its diameter. *Hardenbergia* possesses a root stock structure present at shallow depth but from it a strongly developed root goes down deep into the soil. *Phyllanthus* also possesses a well-defined root stock and a dense clump of roots which, however, remain relatively shallow. *Erechthites* possesses a shallow rooting system. The tree types, *Banksia* and *Eucalyptus* spp. possess both a shallow widely spreading root system and a deeper penetrating one.

Transpiration

The results of a number of transpiration studies are presented in Figures 1 to 8. The purpose is to show the course of transpiration and water balance of elements of the Swan Plain scrub vegetation on passing from spring to the dry summer conditions. Each point in the curves represents the mean water loss of two separate leaves (or in the case of *Hibbertia*, *Bossiaea* and *Phyllanthus*, of small twigs bearing several leaves).

Stirlingia latifolia

This plant is characterised by fairly high transpiration losses when water supply and atmospheric conditions are favourable. In early spring maximum rates as high as 14-15 mg./g./min. have been recorded (Fig. 1A), but in the majority of the experiments the highest values found did not exceed 10 mg./g./min. The average rate (8 a.m. to 5 p.m.) obtained from a number of experiments carried out during early and late spring periods was 4.7 mg./g./min. Rates after the break of season rains in May and on dry days throughout the winter when evaporation was low, remained below those of spring. Passing from late spring into summer, rate of water loss gradually fell, maximum rates recorded being below 4 mg./g./min. in late summer, (Fig. 1B). A daily two-peak curve is characteristic during the dry period and is to be contrasted with the typical single peak curve found in winter and spring experiments. The average daily rate during dry summers was found to lie between 2 and 2.5 mg./g./min. in the University station and was lower (1.2 mg./g./min.) at the Cannington station.

As will be described in more detail later, the rate of water loss from young leaves is much lower than that from mature leaves. As the amount of new growth in *Stirlingia* in a given season is generally small however, and as the reduced transpiration effect tends to be minimized as the spring flush leaves mature in summer it is considered unlikely that water loss differences between young and old leaves exercise any marked influence upon the overall summertime water economy of the plant.

Observations on stomatal opening in mature leaves during spring and early summer months showed some parallelism with transpiration trends while in young leaves there was evidence of a high degree of parallelism. Passing into mid and late summer, mature and maturing leaves of plants at the University station showed much less correspondence between stomatal opening and rate of water loss. On several occasions stomata were found to remain widely open while transpiration was falling. The hydro-reaction of stomata in mature leaves was found by separate experiment to be very sluggish. Stomata towards the base of such leaves were less responsive than those nearer the apical part. Young *Stirlingia* leaves showed an interesting variation in degree of stomatal aperture along their length. In the early afternoon stomata towards the apex of the leaf were closed, those in the mid section were open to a medium degree and those towards the basal part were widely open. In the late afternoon the apical stomata opened widely while those lower down tended to close. Use of the much more delicate *n*-dodecane-nujol infiltration series facilitated the study of these changes. In the more desiccating environment at Cannington during late summer, stomata were frequently found to be closed to isobutyl alcohol throughout the major portion of the day.

The *n*-dodecane series was not then in use, but in the light of comparative tests since carried out it is likely that stomata may have been recorded as open to 2 or 3 of this series. The low transpiration rate recorded may thus represent more than cuticular transpiration.

The water saturation deficit (W.S.D.) was examined in the Cannington experiments and was found to remain low during the day with a maximum of 6.9% and an average of 6.4%. In most experiments in summer similar low W.S.D. values were obtained. An exception occurred in a test plant in February when a maximum of 17.2% and an average of 11.1% for the day, was recorded. The W.S.D. during the spring showed no marked increase during the day indicating that water is absorbed almost as fast as it is transpired. A similar picture was found in early summer, but as atmospheric and soil conditions worsened in late summer, the W.S.D. tended to rise during the morning hours. When a critical low water content was reached, transpiration began to fall. With the building up of water content transpiration rose to give the second peak as illustrated in Figure 1B.

For *Stirlingia* the relatively low value of W.S.D. extending into late summer indicated that even though a large number of the more shallow roots were non-functional due to dried-out soil, the deep main root system ensured that the plant was not subject to great water stress.

Hardenbergia comptoniana

Hardenbergia shows a fairly high transpiration rate in spring when abundant soil moisture is present, but with advancing summer the rate of water loss falls to quite low levels. The transpiration curves in spring are of the one-

peak type and follow approximately the course of evaporation and saturation deficit during the day (Fig 2A). Maximum transpiration rates of about 10 mg./g./min. have been recorded while the daily average lies between 5 and 6 mg./g./min., the peak of the curve generally occurring between 12 noon and 2 p.m. In early summer the peak of transpiration, while approximately of the same magnitude as in spring, is found to occur much earlier in the day. Despite rising evaporation and increasing saturation deficit, the transpiration rate tended to fall to a relatively low and fairly constant level during the day. Later on under the more severe mid-summer conditions the morning peak became much shallower (Fig. 2B) and the water loss during the rest of the day fell to quite low levels (maximum 2.6 mg./g./min., average 1.5 mg./g./min.). The mean daily value from a number of experiments during late summer was 1.3 mg./g./min. Water saturation deficit remained quite low, maximum values not exceeding 8%. This plant with advancing summer limits its transpiration so that water loss is fairly rapidly made good by absorption through the deep root system. There is therefore no difficulty with water balance. The infiltration technique for ascertaining stomatal aperture could not be used in the case of *Hardenbergia*, the leaf being of the heterobaric type.

In late summer, tests of stomatal conductance using the cobalt chloride paper method (Milthorpe 1955) showed very low values associated with low transpiration rates as determined by the torsion balance method. It is likely that during the summer the stomata exercise control over water loss in *Hardenbergia*.

Banksia menziesii and *B. attenuata*

These two species presented a contrast in that while *B. menziesii* showed quite a high rate of water loss in late spring (maximum daily rate 11.5; average rate 7.6 mg./g./min.; Fig. 3A), *B. attenuata* lost water at a much lower rate (maximum 5.2, average 3.5 mg./g./min., Fig. 4A).

Passing into summer *B. menziesii* tended to reduce its transpiration rate to a relatively low level (daily average 1.7 mg./g./min. Fig., 3B) earlier than did *B. attenuata* where the rate in early summer (average 11.1 mg./g./min.) rose well above that recorded in spring (Fig. 4B). It was only in the later part of summer that *B. attenuata* reduced its water loss and even then

the average daily value was high at 4.2 mg./g./min. Considerable difficulty was experienced in endeavouring to obtain a clear picture of water saturation deficit for both species of *Banksia*. Considerable variability was found to exist, even between matched leaves, in their ability to take up water after the 2-3 minutes of exposure needed for initial weighings. It is therefore reported with caution that the maximum value obtained did not exceed 8% in mature leaves and 20% in cutinized but not fully mature leaves.

In both of the above species of *Banksia* the lower surfaces of the leaves are covered with a dense felt of hairs and the infiltration technique of determining stomatal aperture could not be employed.

Hibbertia hypericoides and *Bossiaea eriocarpa*

Hibbertia, a fairly shallow rooting plant and *Bossiaea*, whose root system has been found to penetrate to 4 feet, both possess the small ericoid type of leaf. Owing to the small size of the leaf, transpiration experiments were conducted using twigs with several leaves attached. The rates of transpiration in spring were moderately high (see Figs. 5A and 6A). Transpiration rates increased on passing from spring into early summer, while adequate soil moisture was still present and evaporation was not unduly high. With advancing summer the transpiration rate of both plants markedly declined and by late summer both showed quite low average rates of transpiration (Figs. 5B and 6B). *Hibbertia* in late summer at the University station gave average rates of 2.2 mg./g./min. Under the more desiccating conditions of the Cannington area, leaves of *Hibbertia* plants became very revolute and turned a yellowish colour, water loss being very low. When twigs were cut and placed in water the leaves took up water and recovered their green colour within 2-3 days. This recovery from yellow to normal green occurs in nature after the infrequent summer rains and regularly after the break of season rains. Using the infiltration method stomatal aperture in *Hibbertia* could be followed reasonably well during spring and early summer, but some difficulty was experienced in the really dry period. Recurving of leaf margins and the closer packing of the stellate hairs then made it difficult to ascertain whether the stomata were slightly open or completely closed. The water saturation deficit in *Hibbertia* increased with advancing season. In spring maximum deficits of 9.6% were recorded with an average of 7.3%.

FIGURES 1-8 INCLUSIVE

The following symbols are used throughout these figures:—

T.	◇	Temperature
S.D.	□	Saturation Deficit
E.	△	Evaporation
TR.	— ○ —	Transpiration mg./g./min.
	-- ● --	" "
	-- ■ --	" mg./sq.dm./min.
ST.	-- ● --	Stomatal aperture
	-----	Light intensity

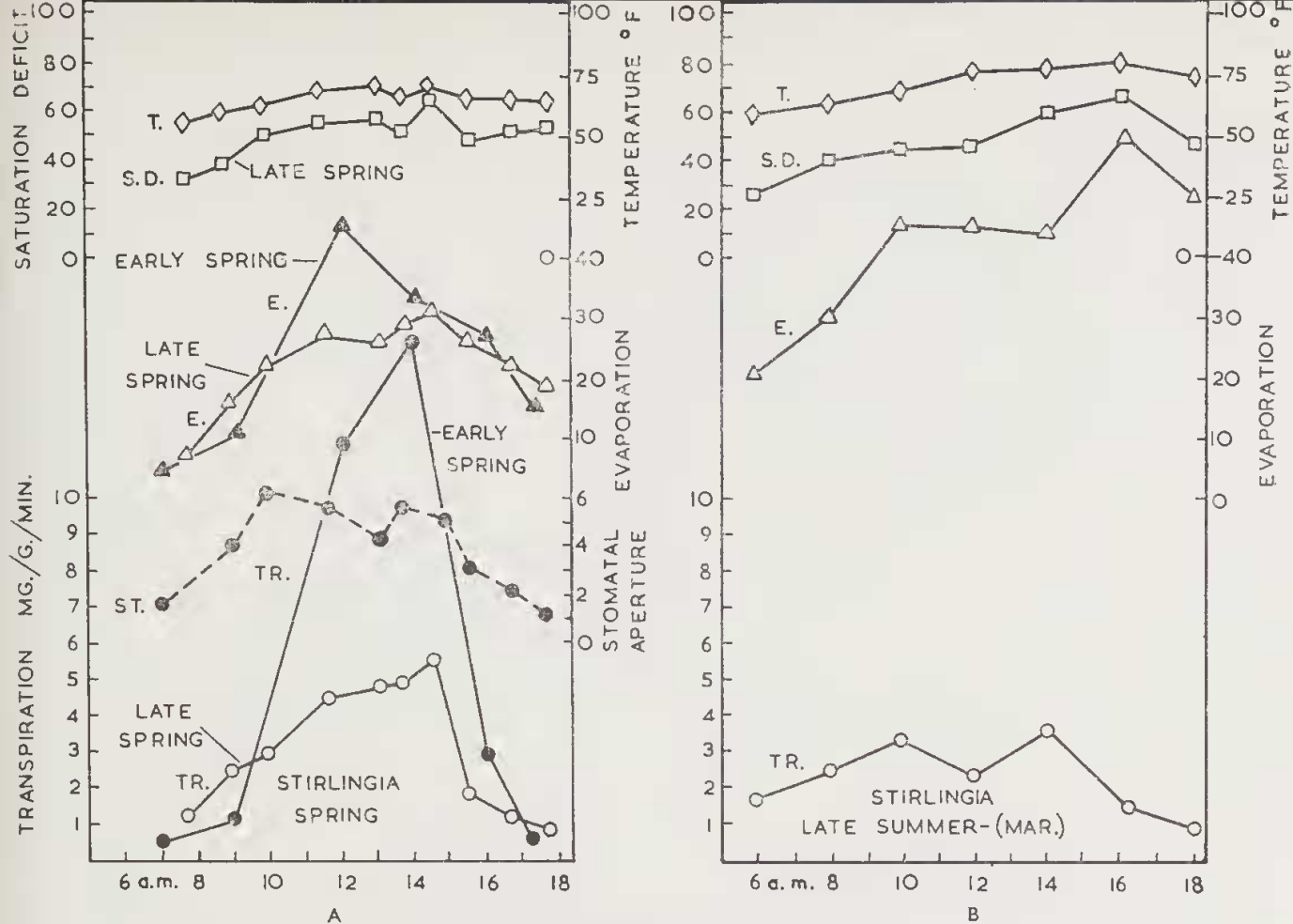


FIG. 1.—Daily march of transpiration in *Stirlingia latifolia*—mature leaves. University Station. (A) Early and late Spring, (B) Late Summer.

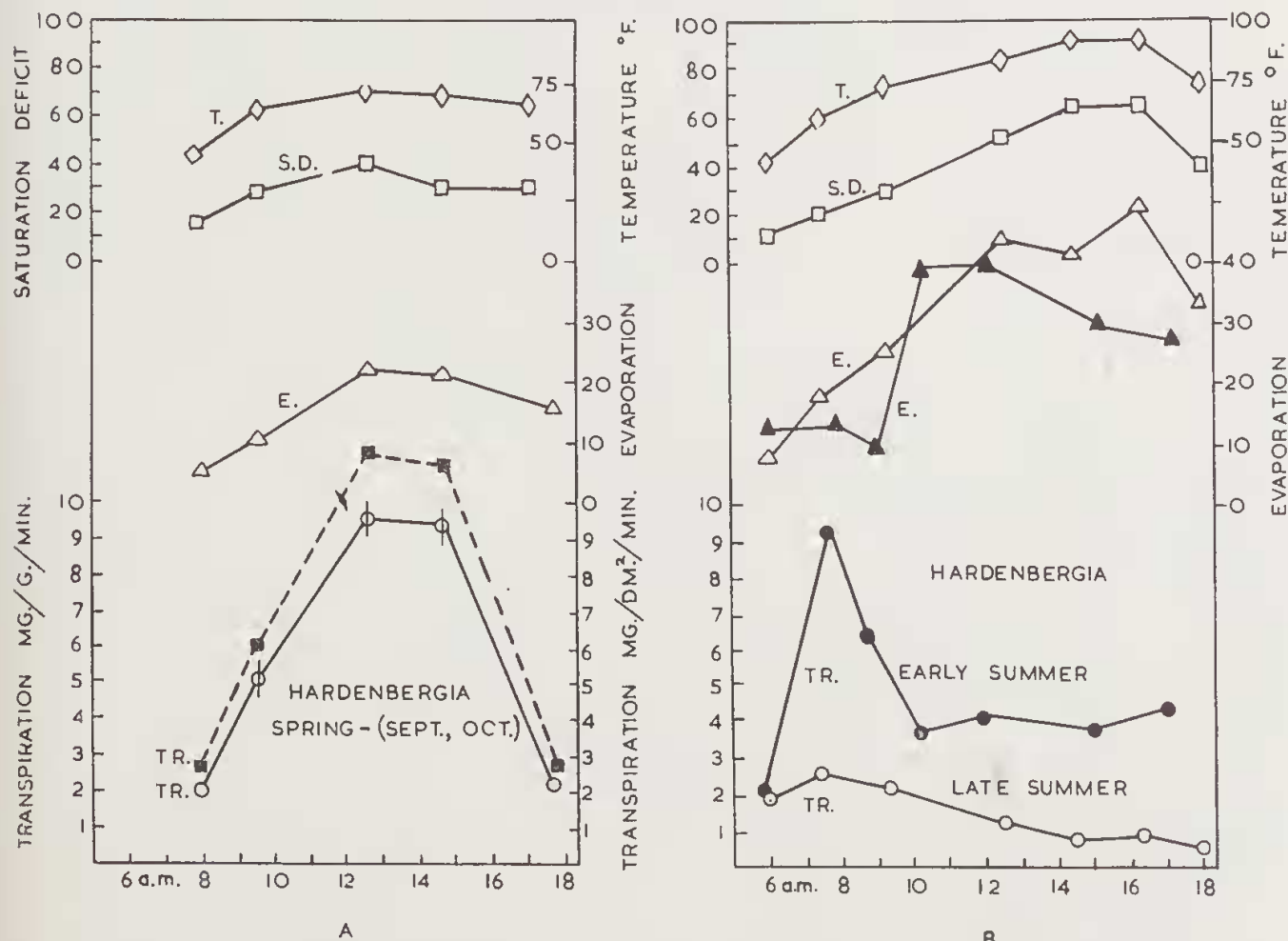


FIG. 2.—Daily march of transpiration in *Hardenbergia comptoniana* in (A) Spring and (B) Early and Late Summer. In Fig. 2B:—Early Summer, \blacktriangle and \bullet Late Summer, \triangle and \circ

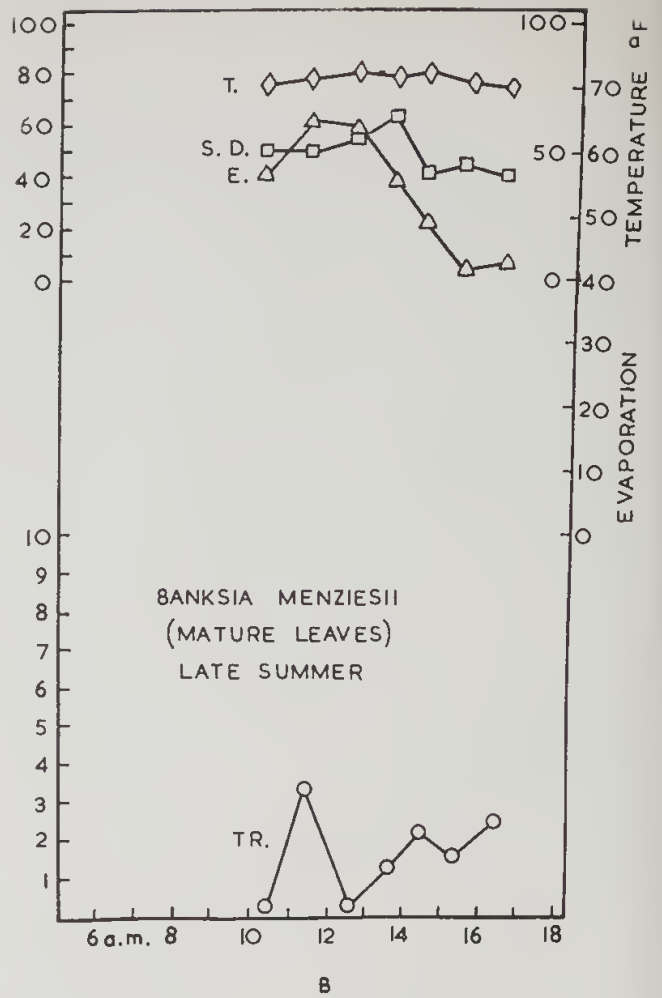
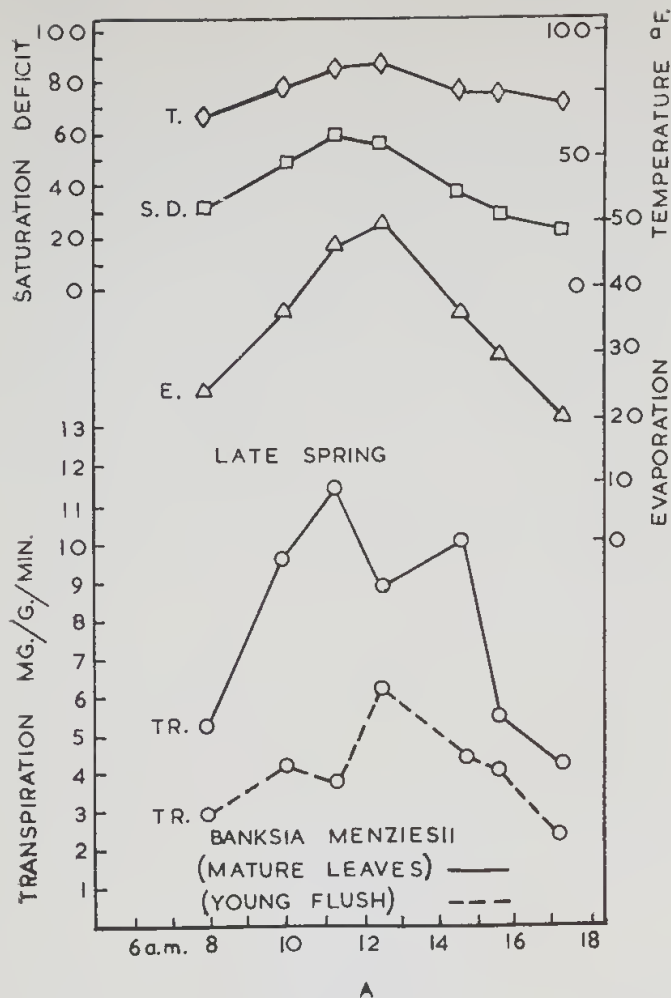


FIG. 3.—Daily march of transpiration in mature and young flush leaves of *Banksia menziesii* in (A) Late Spring and (B) Late Summer.

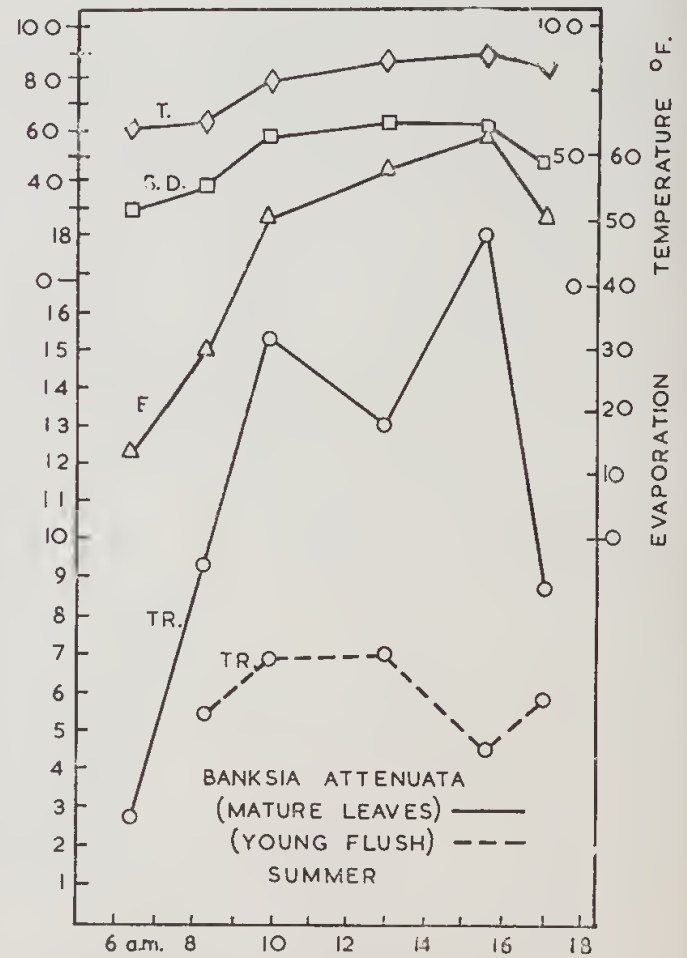
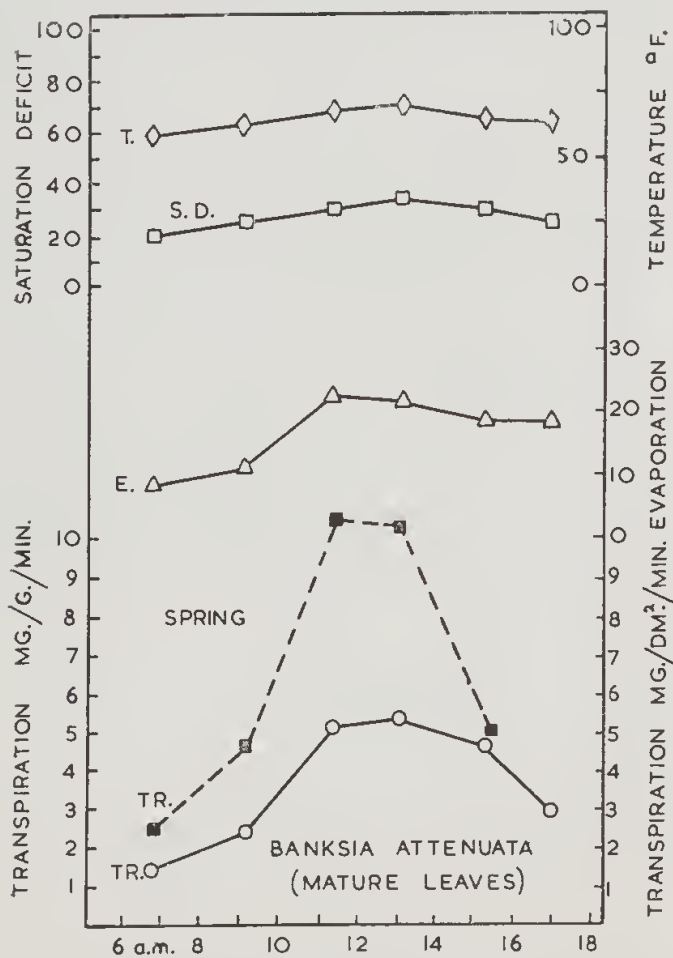


FIG. 4.—Daily march of transpiration in mature and young flush leaves of *Banksia attenuata*, in (A) Spring and (B) Summer.

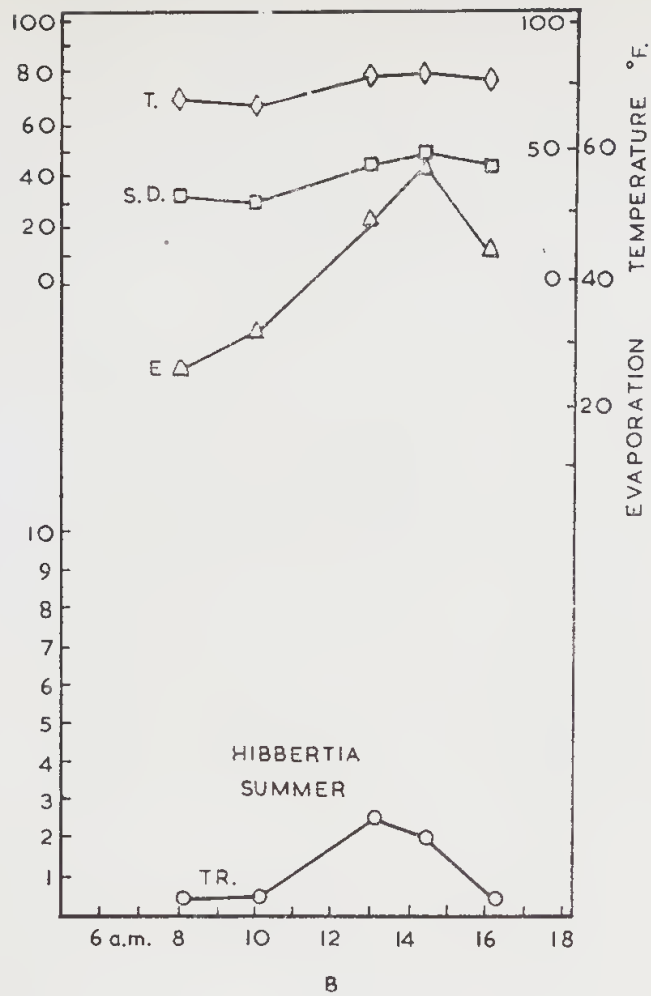
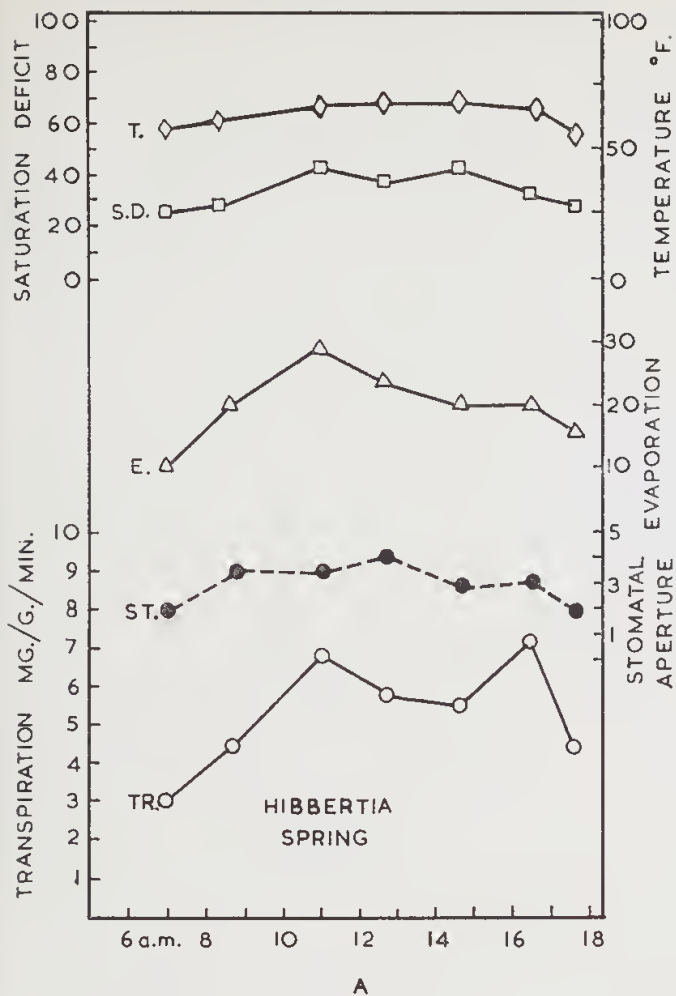


FIG. 5.—Daily march of transpiration in *Hibbertia hypericoides*, in (A) Spring and (B) Summer.

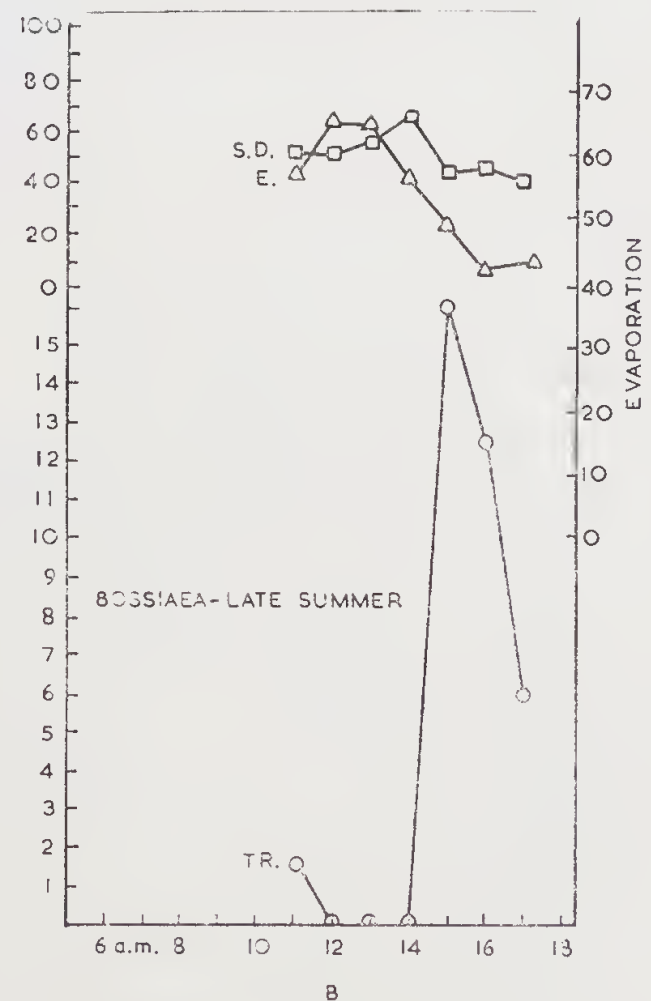
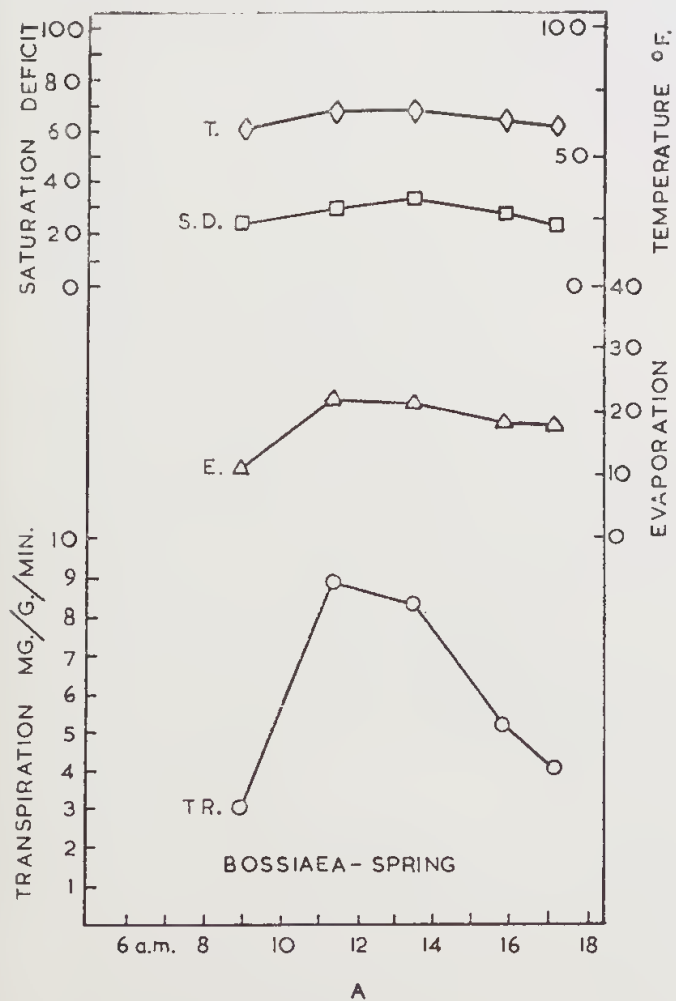


FIG. 6.—Daily march of transpiration in *Bossiaea eriocarpa* in (A) Spring and (B) Late Summer.

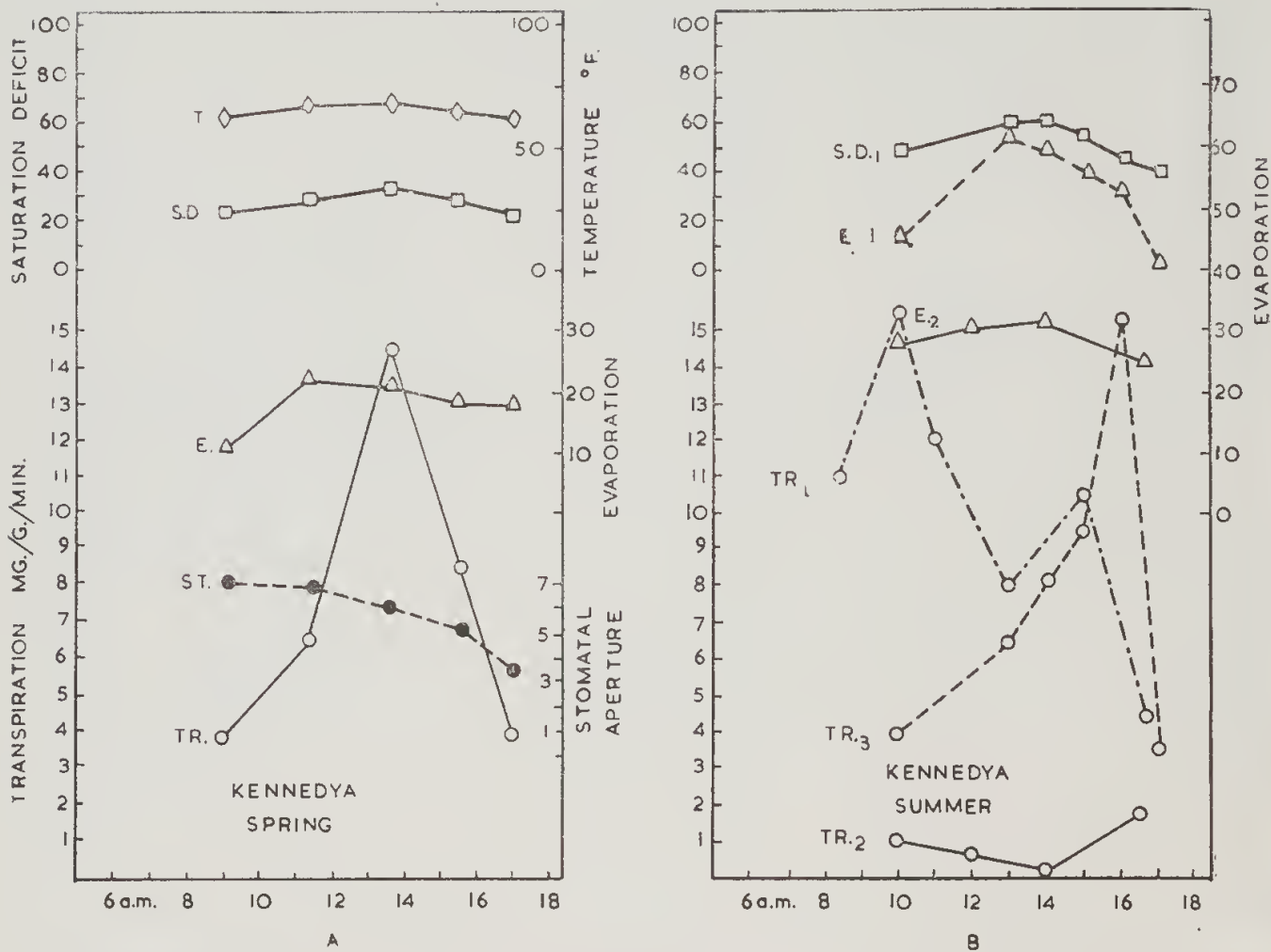


FIG. 7.—Daily march of transpiration in *Kennedyya prostrata*, in (A) Spring and (B) Summer.

Early Summer:—E₁ and TR₁
 Late Summer:—E₂ and TR₂
 Summer (after rainfall):—TR₃

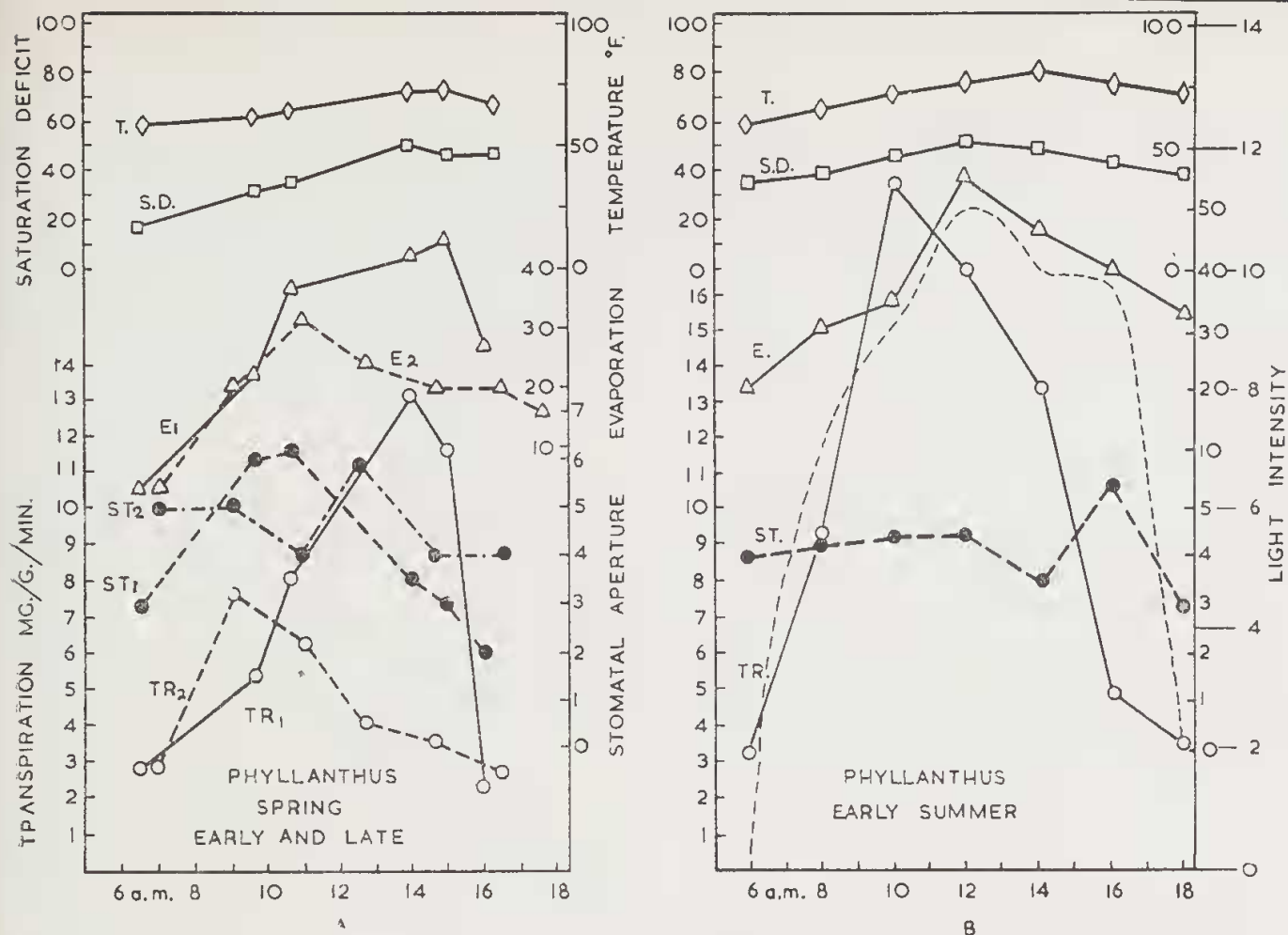


FIG. 8.—Daily march of transpiration in *Phyllanthus calycinus*, in (A) Early and Late Spring, and (B) Early Summer.

Early Spring:—E₁, ST₁ and TR₁
Late Spring:—E₂, ST₂ and TR₂

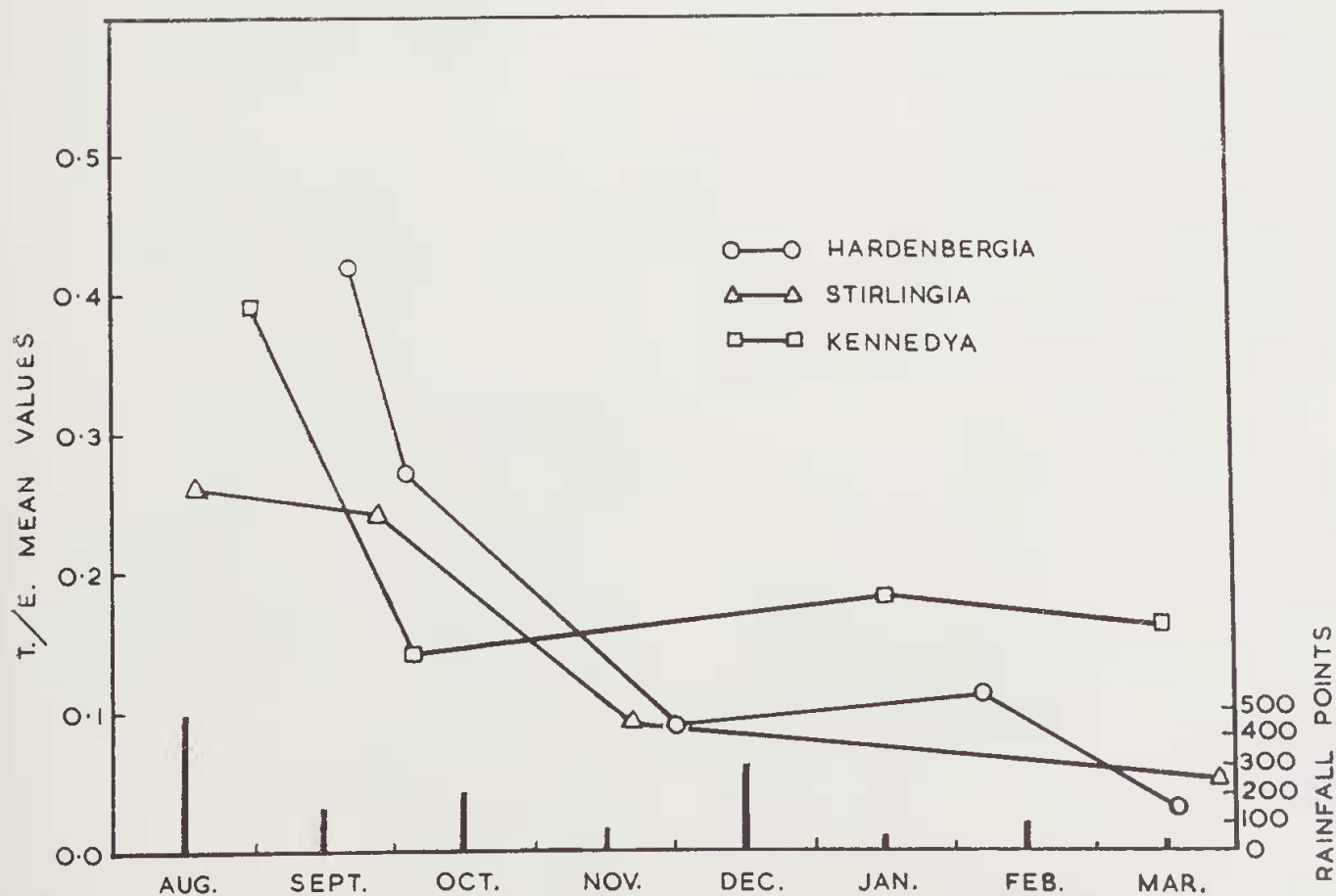


FIG. 9.—Relative transpiration (T/E) of selected plants passing from Spring into Summer, and monthly rainfall data.

In late summer maximum deficits of 25 to 26% were recorded. In spring no significant increase in water saturation deficit occurred during the day indicating that water uptake was keeping pace approximately with transpiration. With advancing summer the water saturation deficit rose during the day, the maximum value often not being reached until 2 or 3 p.m. With the transpiration peak being reached at 8 or 9 a.m. it is clear that during late summer the plant is for some time during each day under considerable stress.

High osmotic values obtained for extracted leaf juice at this time confirm the condition of stress. The plant reacts to this stress by the recurving and incurving of the leaf margins so that the stellate hairs are pressed close together. With closure of stomata water loss is reduced to a low level.

Bossiaea eriocarpa showed the lowest daily average transpiration in late summer of any plant tested in this series, namely 0.3 mg./g./min. For long periods at a time during a hot day no evidence of water loss could be obtained with the torsion balance. The rate might then rise very suddenly, water vapor being released as it were in a burst (Fig. 6B). A close correspondence between stomatal aperture and water loss in *Bossiaea* was established. Where the water loss was negligible, stomata were found to be completely closed to isobutyl alcohol, but when the transpiration burst occurred the stomata could be shown to be open to 1 or 2 of the infiltration series. The stomata of *Bossiaea* react very rapidly in the hydro-reaction test. Within three minutes stomatal apertures have been observed to close down from 5 to 3 on the isobutyl alcohol-ethylene glycol scale; in another three minutes to 1, followed within a further three minutes by complete closure. The water saturation deficit in summer was found to be high with an average of 49% and a maximum of 57%. This, together with the fact that the osmotic value of the leaves rose considerably during the summer months indicated a considerable degree of stress even though some roots have been observed to go down to 4 feet in the sand.

Kennedya prostrata

As may be seen from Fig. 7A, which is typical of several experiments performed, *Kennedya* shows a one-peak curve in spring with high maximum and average daily rates of water loss. Stomata which are present both on the upper and lower surface show gradual closure during the day but appear during this period to have little controlling effect upon rate of water loss. Thus even when transpiration was reduced to 3.8 mg./g./min. at 5 p.m. (Fig. 7A) stomata still remained fairly widely open. Passing into early and mid summer, transpiration rates frequently remained quite high and curves were of the two-peak type. With increasing dry conditions in late summer low transpiration rates were recorded (Fig. 7B, Tr₂). Stomata were closed to isobutyl alcohol series throughout the day. Water saturation deficit values however remained low,

rising only to a maximum value of 9.6%. Rain-fall during any part of the summer rapidly resulted in an increase in the transpiration rate with a tendency to return to the single peak curve. No clear overall relationship between stomatal aperture and water loss could be demonstrated under spring and early summer conditions, but in late summer stomatal closure was an effective factor in reducing water loss. The hydro-reaction of stomata in *Kennedya* was quite rapid.

Eucalyptus marginata and *E. calophylla*

Marked differences were observed in the transpiration rates of these two Eucalypts. *Eucalyptus marginata* (Jarrah) frequently showed a high rate of water loss in summer (average 7.2 mg./g./min.), stomata often being widely open. Under similar conditions *E. calophylla* showed a relatively low rate of water loss (average value 4.2 mg./g./min.) and the stomata during the hotter part of the day were closed to isobutyl alcohol. At such times the rate of water loss was restricted to 0.3 mg./g./min. *E. marginata* may be regarded as being prodigal of water. Due to its deep rooting system adequate water is available even in late summer. *E. calophylla* even though possessing an extensive root system is more sparing of water in summer.

Xanthorrhoea preissii, *Petrophila linearis*, *Daviesia nudiflora*, *Conostephium pendulum*.

These sclerophylls which were growing at the University station were tested from time to time. They showed fairly high rates of water loss in spring but by mid summer the average rates of water loss were markedly reduced.

Phyllanthus calycinus (soft-leaved xerophyte)

Phyllanthus is unusual in having quite thin and soft though small, leaves, and yet occurring as a character plant among the sclerophylls. In late winter and early spring the rate of water loss is high (maximum values of 17.7 mg./g./min. and average daily values of 7.2 mg./g./min. were recorded in August-September). By late spring although the type of curve was still single peaked the time of reaching maximum rate had moved back to much earlier in the day and the peak was lower (Fig. 8A). *Phyllanthus* showed very clear infiltration reactions to both the isobutyl alcohol-ethylene glycol series and the *n*-dodecane-nujol series. In early spring experiments the stomata showed some degree of closure while transpiration rate was still rising. Stomatal aperture then remained relatively constant until late in the day by which time transpiration rate had fallen to quite low levels. In late spring and early summer stomatal apertures were still found to remain at fairly constant aperture while transpiration was rising or falling.

In early summer the rate of water loss remained as high as in late spring, but as atmospheric and soil moisture conditions worsened, defoliation of *Phyllanthus* plants

commenced and continued up the stems until by mid-summer (late January and early February) very few leaves were left. Even at the stage where lower leaves were commencing to yellow and fall, the stomata on all green leaves remained fairly widely open during hot days and closure did not occur until late in the evening. The stomata were characterized by very slow hydro-reactions. Photo-reactions were faster but as cloudless conditions are usual this reaction appears to have no ecological significance.

The water saturation deficit of green leaves still attached, while defoliation was occurring lower down on the stem, showed low values up to 2.8%. Owing to the fact that a milky latex is present in *Phyllanthus* and that this may have affected water uptake in the saturating experiments, the above low values must be viewed with caution. It seems significant, however, that leaves of *Phyllanthus* although so soft and thin, do not show wilting.

From these results it appears that *Phyllanthus* is prodigal in the use of water and only balances its water budget and survives the summer by drastically reducing its transpiring surface.

Erechthites hispidula (mesomorph)

The water loss of *Erechthites hispidula* a soft-leaved mesomorph growing at the University station was tested for comparison with the sclerophylls. It showed very high transpiration rates through spring (average 10.7 mg./g./min.) and summer (average 13.3 mg./g./min.), up to the time when it wilted irreversibly and died. Stomata appeared to have little controlling influence on transpiration throughout the major portion of the day.

Rate of Water Loss in Mature versus Young Leaves

In the course of preliminary transpiration experiments using leaves from different parts of *Stirlingia*, it was observed that the rate of water loss was much higher from mature leaves than from young leaves of the current season flush of growth.

As this ran counter to the commonly expressed view in transpiration literature that young leaves transpired faster, further studies were made of *Stirlingia* and the work was extended to include the two species of *Banksia*. These further tests confirmed the original observation and it was found that the mature leaves lost water at a much higher rate (both in terms of fresh weight and area) during the hotter parts of the day in spring and early summer (see Figs. 3 and 4 and Table III). With advancing summer the spring flush of leaves gradually assumed the normal highly sclerophyllous form and the differences between the rates of water loss became less apparent.

TABLE III

Rate of Water Loss From Young and Mature Leaves

				Spring.	Early Summer
				mg./g./min.	mg./g./min.
<i>Stirlingia latifolia</i>	Young	6.8	7.2
		Mature	12.6	12.3
<i>Banksia menziesii</i>	Young	4.5	4.0
		Mature	9.0	11.0
<i>Banksia attenuata</i>	Young	2.0	7.0
		Mature	4.9	15.8

The lower rate in the young leaves is due, at least in part, to the better stomatal control associated with greater mobility of their guard cells before the processes of lignification and cutinization develop too far. Experiments described earlier dealing with the degree of stomatal aperture in young versus old *Stirlingia* leaves during the day, showed that young leaves were much more responsive to changes in atmospheric conditions and in water content of leaves. The hydro-reactions of mature leaves were also very sluggish as compared with those of young leaves.

Cuticular Transpiration

Cuticular transpiration in *Hardenbergia*, *Hibbertia*, *Bossiaea*, and *Eucalyptus* species tested in early summer was found to be quite low, varying from 0.1 to 0.3 mg./g./min. The ratio of cuticular to overall transpiration was highest in *Eucalyptus calophylla* (1 : 60). The lowest ratio under the conditions of these experiments was found in *Banksia attenuata* (1 : 36). Owing, however, to the difficulty for *Banksia* of completely covering the felted hairs on the lower surface with vaseline, (particularly near the recurved leaf margins) it is believed that the water loss recorded may not have been completely restricted to cuticular transpiration. Of the above listed sclerophylls it has been shown for *Hibbertia*, *Bossiaea* and *Eucalyptus calophylla* that they can completely close down their stomata under desiccating conditions. The first two named also achieve more efficient protection by strong leaf inrolling. Thus with low cuticular transpiration, water loss may be reduced to a minimum. *Stirlingia* and *Kennedya* which bear stomata on both leaf surfaces could not be satisfactorily tested for cuticular transpiration. It may be noted, however, that mature *Stirlingia* leaves are heavily cutinized on both surfaces and it seems reasonable to assume that where stomata do close completely under late summer conditions cuticular transpiration would be slight. *Kennedya* leaves are lightly cutinized on the upper surface and dense hairs are present on the lower surface. Under desiccating conditions the leaf margins tend to roll upward and inward. Transpiration experiments in late summer where stomata were recorded as closed to isobutyl alcohol, showed a fairly high transpiration rate early in the morning. This declined progressively until 2 p.m. with rising evaporation. Subsequent tests suggested that the stomata would have been open to at least 3 on the more delicate *n*-dodecane-nujol series at the start of the

experiment and that gradual closure would have occurred associated with some decline in the rate of water loss. The hairs on the lower surface would further help to reduce transpiration and the upward and inward rolling of the leaf would also give some protection to the upper surface. Their combined operation would tend to offset the lack of cuticular development in *Kennedya* and would result in the low transpiration rate recorded.

Course of the Transpiration Curves

Examination of the spring curves plotted in Figs. 1 to 8 shows that with adequate moisture in the soil at all levels and favourable climatic conditions, transpiration in general is high. The curves tend to run parallel to those for evaporation and atmospheric saturation deficit. Passing into summer, with increasing evaporation, higher atmospheric saturation deficits and drier soil, transpiration of the sclerophylls is seen to be gradually restricted. In the case of *Hardenbergia* and *Hibbertia* the late summer curves are of the one-peak type and fall as evaporation rises during the later morning and early afternoon hours.

Stirlingia, *Kennedya*, *Bossiaea* and *Banksia* show two-peak curves. The first is in the early morning then with rising evaporation the rate of water loss drops. The second peak in the afternoon may occur while evaporation is still either rising, maintaining a high level, or falling. The increased rate of water loss at this time may be associated with a build up of water content in the leaf tissues but it was not possible to obtain evidence of this.

When relative transpiration, T/E (used in a restricted sense) was plotted against month of year, commencing in spring, the decreasing transpiration with passage into summer became apparent (Fig. 9). It is noteworthy that the steepest fall in relative transpiration occurs by early summer. By this time the soil at the University station at the 2 foot level is drying out (moisture content 1.3%, suction force 50 atmospheres). This affects a large part of the root system of all the plants tested. The shallow rooting *Hibbertia* and *Phyllanthus* and to a lesser extent *Bossiaea* suffer from some water lack at this stage. *Stirlingia*, *Hardenbergia*, the banksias and the eucalypts all possess as well a deep rooting system. In all cases, however, with the exception of *Eucalyptus marginata*, restriction of transpiration occurred with rising evaporation giving low values for T/E. With more desiccating atmospheric and soil conditions passing into late summer, *Hibbertia* passed into a state of anabiosis, while *Phyllanthus* retained only a few yellowish leaves. *Kennedya* after the first drop, maintained fairly high T/E values passing into late summer, while *Hardenbergia* and *Stirlingia* fell to rather low levels.

Osmotic Values

Detailed observations on the osmotic values of leaves of sclerophylls will be reported elsewhere. It will suffice here to note that osmotic values rose with advancing summer while in general a rapid return to lower values occurred

with break of season rains. *Hibbertia* showed the highest values at 25-27 atmospheres. Possibly higher values would have been obtained in later summer but the leaves were so dry that, with the existing sap-press, juice could not be squeezed from them. *Bossiaea* also gave high values up to 21 atmospheres. Here again higher values would no doubt have been obtained in late summer if sap could have been extracted from the leaves.

Stirlingia, *Banksia* and *Kennedya* gave values up to 21 atmospheres (in one instance a value of 28 atmospheres was recorded for *B. menziesii*) and sap could still be extracted although with some difficulty throughout the summer. Osmotic values up to 16 atmospheres were recorded for *Hardenbergia* in late summer. The figures for *Hibbertia* and *Bossiaea* taken together with the dry nature of the leaves and the high water saturation deficit mentioned earlier, suggest a strained water balance in late summer. The values for the deeper rooting *Stirlingia* and *Hardenbergia* were not unduly high. This fact, together with the lower water saturation deficit observed in these plants, suggests that they possess a reasonably balanced water budget.

Soil Moisture and Soil Suction Force

Soil moisture values showed continuous decline from spring into summer while soil suction force rose. Typical results at 1 foot depth are given in Table IV.

TABLE IV

Soil Moisture and Soil Suction Force at 1-foot Depth

		Sept.	Nov.	Dec.	Jan.	Feb.
Soil Moisture (%)	University ..	3.0	1.8	1.4	1.35	1.3
	Cannington ...	4.1	1.6	...	0.3	...
Suction Force (Atm.)	University	4.5	...	28.1	42.5	50.0
	Cannington ...	3.8	7.6	...	>100	...

At a depth of 2 feet the moisture content at the University station had by late January fallen to 1.09% and the suction force risen to 75 atmospheres.

For shallow rooting plants—in particular *Hibbertia* and *Phyllanthus*—the decrease in soil moisture and increase in soil suction force has considerable significance. By late summer the suction force at the 2 foot level was reaching values which made it impossible for the plants to absorb water. *Hibbertia* whose roots lay in this zone, after progressively reducing its transpiration loss to low values passed into an almost anabiotic state, while *Phyllanthus* having gradually lost more and more leaves as soil and atmospheric conditions worsened, passed the summer in a defoliated state.

With increasing depth the moisture content of the soil at the University station in late summer remained high as the values in Table V indicate.

TABLE V

Soil Moisture at University Station, Late Summer

Depth of Soil Sample	Soil Moisture (%)	Suction Force (Atm.)
1 foot	1.3	50
4 feet	2.5	10
11 feet	4.0	Zero

The main roots of *Stirlingia* and *Hardenbergia* have been traced down to 8 feet in sandy soil and judging from their thickness at that depth could well continue down several feet further. Clearly although the surface lateral roots may be put out of action by rising suction forces at the two foot level, the possession of a deeper penetrating main root means that these plants are unlikely to suffer from severe water stress. The reduction in transpiration rate in summer may be related to slower water movement through the diffuse porous vessels of the deep growing main root with its subsidiary lateral system.

Discussion

All of the sclerophylls examined with one exception, were found to reduce their rate of water loss when passing into the dry summer period irrespective of whether they were (a) relatively shallow rooting types as in *Hibbertia* and *Bossiaea*, or (b) ones which possessed a combination of shallow and deeper extending roots as in *Stirlingia*, *Hardenbergia* and *Kennedya*, or (c) the trees *Banksia menziesii*, *B. attenuata* and *Eucalyptus calophylla*.

Plants of type (a) are clearly sensitive to soil drought, while types (b) and (c) are only partially affected. *Eucalyptus marginata* alone among the sclerophylls so far examined, maintained a high level of water loss during summer. The shallow rooting soft-leaved xerophyte *Phyllanthus calycinus* and the mesophyte *Erechtites hispidula* also showed no tendency to restrict water loss with advancing season, but under conditions of soil drought almost complete defoliation occurred in the former, while in the latter case the plant finally died.

Comparative studies of water loss of sclerophylls during different seasons are not available for other parts of Australia, but Wood (1923, 1924) has worked on the transpiration of sclerophylls during summer in arid inland South Australia. He showed that while there was considerable individual variation, their average rates of water loss were low (*Eremophila scoparia* 1.15 mg./sq.dm./min.; *Casuarina lepidophloia* 2.25 mg./sq.dm./min.; *Acacia aneura* 1.38 mg./sq.dm./min.). The mesophyte *Senecio magnificus* showed a rate of water loss well above that of all sclerophylls in the area. This high rate of water loss is paralleled by that of the mesomorph, *Erechtites hispidula* in the Swan Plain area. The rate of loss for this mesomorph is far higher during spring and summer than that of any Swan Plain sclerophyll tested. Under the field conditions near Perth the xerophytic sclerophylls therefore do not conform to Maximov's experience at Tiflis (1929). Wood (1934) how-

ever, found high values for three Mount Lofty sclerophylls, *Eucalyptus leucoxydon*, *Acacia pycnantha* and *Hakea rugosa*. In field studies of similar types of plant in Victoria and Western Australia, the author has so far not found such high values (Grieve, 1955).

In other areas of Mediterranean climate many investigations on sclerophylls and associated plants have been made. The sclerophylls of the Swan Plain are similar in their water loss behaviour in summer to those from Rovigno (Rouschal, 1938), Palestine (Oppenheimer, 1932, 1953) and Algeria (Killian, 1931, 1932).

The osmotic values of Swan Plain sclerophylls so far examined agree fairly well with Braun-Blanquet and Walter's (1931) statement that optimum figures lie between 18 and 26 atmospheres. No exceptionally high osmotic values such as Rouschal (1938) and Oppenheimer (1953) record for two or three maquis type shrubs, have so far been found. The values obtained by Wood (1934) for sclerophylls in the Mount Lofty area near Adelaide agree quite well with those obtained near Perth. As might be expected Wood obtained considerably higher values for sclerophylls of arid inland South Australia.

The rise in osmotic values of Swan Plain sclerophylls on passing from spring to summer is similar to that recorded for sclerophylls in the Mediterranean area (Rouschal (1938); Oppenheimer (1953)).

Oppenheimer (1932, 1953) distinguishes four types of Mediterranean maquis vegetation, based on their water balance. Of these we may name three into which most Swan Plain sclerophylls and associated plants fit:

- 1.—*Deciduous plants failing to show appreciable stress throughout the summer*—In the Mediterranean area trees occur in this class, but the closest Swan Plain equivalent is the soft-leaved xerophyte, *Phyllanthus calycinus* which avoids stress by defoliating during summer.
- 2.—*Evergreen trees and shrubs physiologically active throughout the summer*—*Eucalyptus marginata* is the only sclerophyll so far worked on in the Swan Plain area which fits into this group. It maintains a fairly high rate of water loss.
- 3.—*Evergreen species restricting their physiological activity considerably thus avoiding losses of irreplaceable water, and finally reaching a state of near dormancy*—The two relatively shallow rooting genera, *Hibbertia* and *Bossiaea* fit well into this category. Both reduce their water loss drastically in late summer, have high water saturation deficits and high osmotic values. *Hibbertia* in particular passes into a condition of apparent anabiosis until the break of season rains.

It seems that the Swan Plain sclerophyll types such as *Stirlingia*, *Hardenbergia*, and *Eucalyptus calophylla*, which possess a shallow and a deep rooting system, which have medium water saturation deficits and medium osmotic values, but which do not go into dormancy during summer, must form a separate group. They appear to come within Rouschal's Group 2 (1938) in that control of water loss by stomatal closure, or by the operation of some other internal factor, occurs even when adequate moisture is available in the soil, at least to the deeper penetrating part of the root system.

The findings of von Guttenberg (1927) and of Oppenheimer (1953) that stomata of the sclerophyllous evergreens remained wide open in spring, but practically closed during the day in a dry summer, could not be duplicated for all groups of Swan Plain sclerophylls. It is true that *Hibbertia* and *Bossiaea* may close their stomata completely, but in *Stirlingia* the stomata frequently remained open during hot days at the University station, while water loss was reduced. Only under the more desiccating conditions in late summer at Cannington were the stomata of *Stirlingia* found to be closed during most of the day. This at least suggests that once conditions become too extreme closure of stomata takes place and only cuticular transpiration occurs.

The difference in rate of water loss between young flush and mature leaves of sclerophylls appears to have been observed hitherto only by Henrici (1946) in South Africa, although Rouschal (1938) did show similar differences between one year old and two year old leaves of sclerophylls at Rovigno. Henrici noted that for the introduced *Eucalyptus stuartiana* on

bright days the young leaves always transpired less than the old. Owing to the fact that adequate soil moisture was present at all times on hot days during her experiments, the results do not appear to be explainable on the grounds of difference in stomatal behaviour between the young flush and mature leaves as is the case in the Swan Plain sclerophyll, *Stirlingia*.

The difficulties encountered in determining water saturation deficits in some sclerophylls have been indicated. These difficulties affected also the attempt to apply the concept of sub-lethal deficits (Oppenheimer 1932, Rouschal 1938) to indicate relative drought resistance in Swan Plain sclerophylls. Inconclusive results for mature leaves of *Banksia* and *Stirlingia* were obtained because very often the leaves either failed to absorb water or absorbed it irregularly. It was observed that even with petioles in water rapid death of such leaves often occurred. Before reaching the conclusion that *Banksia* and *Stirlingia* have a low degree of drought resistance from such results, further experiments on infiltrating such leaves under pressure need to be done. *Hardenbergia* presented no difficulties with water uptake by leaves and the sub-lethal deficit here indicated that this plant would have a high degree of drought resistance.

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